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Vertical migration of *Onychiurus subtenuis* (Collembola) in relation to rainfall and microbial activity

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With 3 figures

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1. Introduction

Dispersal of microbial spores by the soil fauna has long been considered an important interaction that could alter microbial community structure, patterns of succession and decomposition rates. (Earlier literature comprehensively reviewed by Visser 1985).

As movement of microbial propagules due to purely physical forces within the litter-soil profile is predominantly downwards, upward movement of the fauna that could potentially carry spores is particularly important. Such movements have been well documented on a seasonal scale (e.g. Dowdy 1944; Hale 1966 and Usher 1970) and are thought to be related to micro-meteorological conditions. For some Collembola statistically significant relationships between vertical distribution and monthly precipitation rates or soil moisture conditions have been established (Marshall 1974; Takeda 1978) indicating that some species descend further down the profile as the surface layers dry out, presumably to avoid desiccation. However as Hågvar (1983) points out, food availability may become a limiting factor at lower levels. It thus appears that vertical migration is a way of maintaining a balance between the higher mortality in the drier upper layers and reduced reproductive output resulting from the less favourable feeding conditions, in the lower layers.

The time scale of these migrations has not yet been fully resolved. Most previous work has been based on seasonal or monthly changes in distribution; however Whitford *et al.* (1981) have shown that in desert ecosystems mites, Collembola and nematodes all react very quickly to simulated rainfall, increasing significantly in the litter within an hour after it has been moistened. Bauer (1979) has furthermore clearly demonstrated that two epigeal species of Collembola climb up tree trunks rapidly after rainfall to feed on epiphytic algae.

Therefore as part of a larger study of interactions between *Onychiurus subtenuis* (Folsom) and soil fungi in a cool temperate deciduous forest, observations were made on changes in the vertical distribution of this collembolan. Up to 4.7×10^3 m^{-2} *O. subtenuis* were observed in the litter layer of this *Populus tremuloides* Michx. woodland by Parkinson, Visser & Whittaker (1979) during spring snow melt, when their selective grazing was found to alter substantially the competitive balance between two colonizing fungi. As the surface layers dry out during the summer the *O. subtenuis* migrate deeper into the fermentation and humus layers. Rainfall in this area is low during the summer and mostly concentrated into periodic heavy storms. Within 12 h of such rain collembola were again observed up in the surface litter layers. This study was undertaken to investigate changes in the vertical distribution following summer rains and to clarify the reasons for the migration using laboratory experiments.

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2. Material and methods

2.1. Field studies

The study site was in an aspen poplar woodland located at 1,400 m in the front range of the Rocky Mountains, Alberta, Canada (51° 2′ N 115° 4′ W). Full details of the study site have been presented by LOUSIER & PARKINSON (1976).

At each of four sampling times eight 54 mm diameter 10 cm deep soil cores were removed from the organic profile at 1 m intervals along a transect 4 m from the southern border of a sampling grid described by LOUSIER & PARKINSON (1979). Cores were sealed in polyethylene tubes and transported to the laboratory where they were immediately subdivided into the 4 constituent litter layers. The layers, consisting of the litter (L), fermentation 1 (F_1), fermentation 2 (F_2), and humus (H), were separated according to the criteria outlined by VISSER & PARKINSON (1975).

After obtaining the fresh weight of each sample, the soil fauna were extracted using a modified MACFADYEN high gradient extractor described by ADDISON & PARKINSON (1978). Counts of *O. subtenuis* were made while the animals were still active on the surface of the water contained in the extractor canisters. Following the extraction, moisture contents were determined by drying samples to constant weight at 80 °C. Rainfall data were obtained from the Kananaskis Environmental Research Station located 2 km from the study site.

2.2. Laboratory studies

In order to clarify the reasons for the vertical movements observed in the field, artificial litter profiles were constructed in laboratory microcosms. The containers consisted of cylinders made of 2 mm thick glass, 120 mm long and 49 mm internal diameter, containing a 16 mm thick plaster of Paris base and topped with a piece of perforated polythene. The organic profile consisted of 30 mm of humus on the plaster of Paris base with the laminae of 10 *P. tremuloides* leaves stacked horizontally above it.

The humus was collected from the study site in August, dried to 7.5% moisture in soil fauna extractors to remove all animals, then stored dry until October, when it was restored to the 67% moisture content it had when removed from the field in August. 15 mm of moist humus were then placed on the plaster of Paris base of each microcosm and 75 *O. subtenuis* introduced, followed by a further 15 mm of humus. The collembola were left for two days to disperse in the humus and then the leaf laminae were placed on the surface and the microcosms kept at 14 °C in darkness until the next day when the leaves were removed carefully and the number of *O. subtenuis* on each surface counted. The leaf surfaces were assigned scores of from 1 for the underside of the bottom leaf to 20 for the upper side of the top leaf and an index of the average height animals had climbed in each microcosm was calculated from

$$\text{Height index} = \sum_{i=0}^{i=20} \frac{\text{Leaf surface score} \times \text{number of Collembola on surface}}{\text{Total number in litter}}$$

The Collembola introduced into the microcosms were extracted alive from large samples of litter collected during October, kept for up to 3 days in jars lined with moist plaster of Paris and fed *Cladosporium* and dried bakers' yeast.

Following preliminary pilot experiments five different litter treatments were used in the first full experiment, each treatment being replicated six times. The first two treatments were designed to recreate, in a simplified form, conditions following a storm, compared with the normal dry summer conditions in the litter. These were:

(1) 'Dry litter' which was collected in August, dried to 10% moisture content in tullgren funnels, stored until October and then moistened to 29% water content which was the moisture content of the litter when the 'dry' October sample was taken. It was kept at 29% moisture for 13 days.
(2) 'Moist' litter collected and dried as in (1) but saturated with sterile distilled water before being stored wet for 13 days.

The other three treatments in this experiment were designed to test whether the Collembola were simply moving into any physically suitable moist habitat available (the control, treatment 3) or whether they were specifically attracted into moist litter with a thriving microflora (treatments 4 and 5) and to see whether the layer from which the microflora originated affected the extent to which they moved. These treatments were:

(3) Autoclaved; litter treated as for (2) but autoclaved after saturating it with distilled water.
(4) Litter microflora as for (3) except that after autoclaving the litter was soaked in an inoculum of litter microflora, made by homogenizing 5.0 g of fresh moist litter with 100 ml of sterile distilled water, before being left for 13 days for the micro-organisms to grow.
(5) Humus microflora as for (4) except that the humus inoculum was made by mixing 10 g humus in 100 ml sterile distilled water.

The second experiment was designed to clarify more precisely whether the Collembola responded differently to different groups of micro-organisms. In this experiment the control consisted of leaves

autoclaved as in (3) above and 5 experimental treatments of autoclaved litter soaked in inocula of (1) bacteria, (2) yeast, (3) *Cladosporium*, (4) *Mortierella* and (5) Basidiomycete 290. Inocula were prepared by culturing and isolating the different microorganisms from the *P. tremuloides* litter on malt extract agar, then scraping them from the agar surface and suspending them in sterile distilled water. Each treatment in this experiment was replicated five times.

3. Results

3.1. Field studies

The vertical distribution of *O. subtenuis* in the litter profile on four different occasions are presented in Fig. 1. The dates were chosen to follow long dry periods in July and October and two periods of rain in July and August. The rain increased moisture content of the litter layer from 29 % to 62 % and of the F_1 from 54 % to 72 % while the F_2 and H layers remained at approximately 70 % throughout. *O. subtenuis* was present at an average population density of $(21.7 \pm 0.9) \times 10^3$ m^{-2} over the sampling season. During the period of low rainfall in July most Collembola were in the H layer (48 %) with only 0.7 % of the population in the L layer. However following rainfall, both immature and adult Collembola were observed to migrate up the profile so that in the second sample following three days of wet weather there were 1.35×10^3 m^{-2} (6.5 % of the population) in the litter layer and only 29 % left in the humus layer. As the litter dried out again in October *O. subtenuis* returned to the F_2 and H layers leaving only 166 m^{-2} (0.8 %) in the litter layer. Using USHER's (1970) index of mean depth and data for average depths of the layers from VISSER & PARKINSON's (1975) study of this site, movement of the adult population was from a mean depth of 4.84 cm on 22. 7. 1980 up to 4.41 cm and 4.36 cm on the two dates following rain storms, then down again to 5.22 cm in the subsequent dry October period.

These results confirmed the initial observation of rapid movement by *O. subtenuis* into wet litter after rainfall but do not explain the reasons for such migrations. To determine whether they were made simply in response to an increase in physically suitable habitat or in response to microbial activity in the L layer, it is necessary to consider the results of experiments with artificial litter profiles constructed in the laboratory.

3.1. Laboratory studies

The distribution of *O. tenuis* in the litter profiles 18.5 h after the start of the first experiment are shown in Fig. 2 and Table 1. Comparing the 'dry' and 'moist' treatments, three times as many Collembola had migrated into the 'moist' litter and had climbed higher up the profile than those in the 'dry' microcosms. Thus vertical migrations similar to those observed following summer rains in the field were taking place in these simplified laboratory microcosms.

A comparison of the autoclaved control with the reinoculated litter treatments shows that this is not simply dispersal into physically suitable habitat: although the autoclaved leaves were just as wet as the reinoculated ones, significantly fewer animals migrated into them than into those incubated with litter or humus microflora ($t = -2.32$ $P < 0.05$ and $t = -3.14$ $P < 0.02$ respectively). It is also clear from Fig. 2 that most of those in the autoclaved profile remained on the lowest surface adjacent to the humus where micro-organisms from the humus would be starting to colonize this substrate. There were slightly more *O. subtenuis* on the leaves inoculated with litter microflora than on those inoculated with humus microflora, but in the latter case they moved slightly higher up the profile. However neither difference was statistically significant.

Since these inocula contained a wide variety of micro-organisms, the second experiment was designed to determine how *O. subtenuis* responded to more specific microbial groups. It was conducted six weeks later than the first experiment after which all litter was removed. During this time the collembola were left in the moist humus layers of the microcosms where they reproduced. The results shown in Fig. 3 and Table 2 are similar to those of the first experiment in that fewer animals (31.6 ± 4.5) migrated into the control autoclaved litter (A)

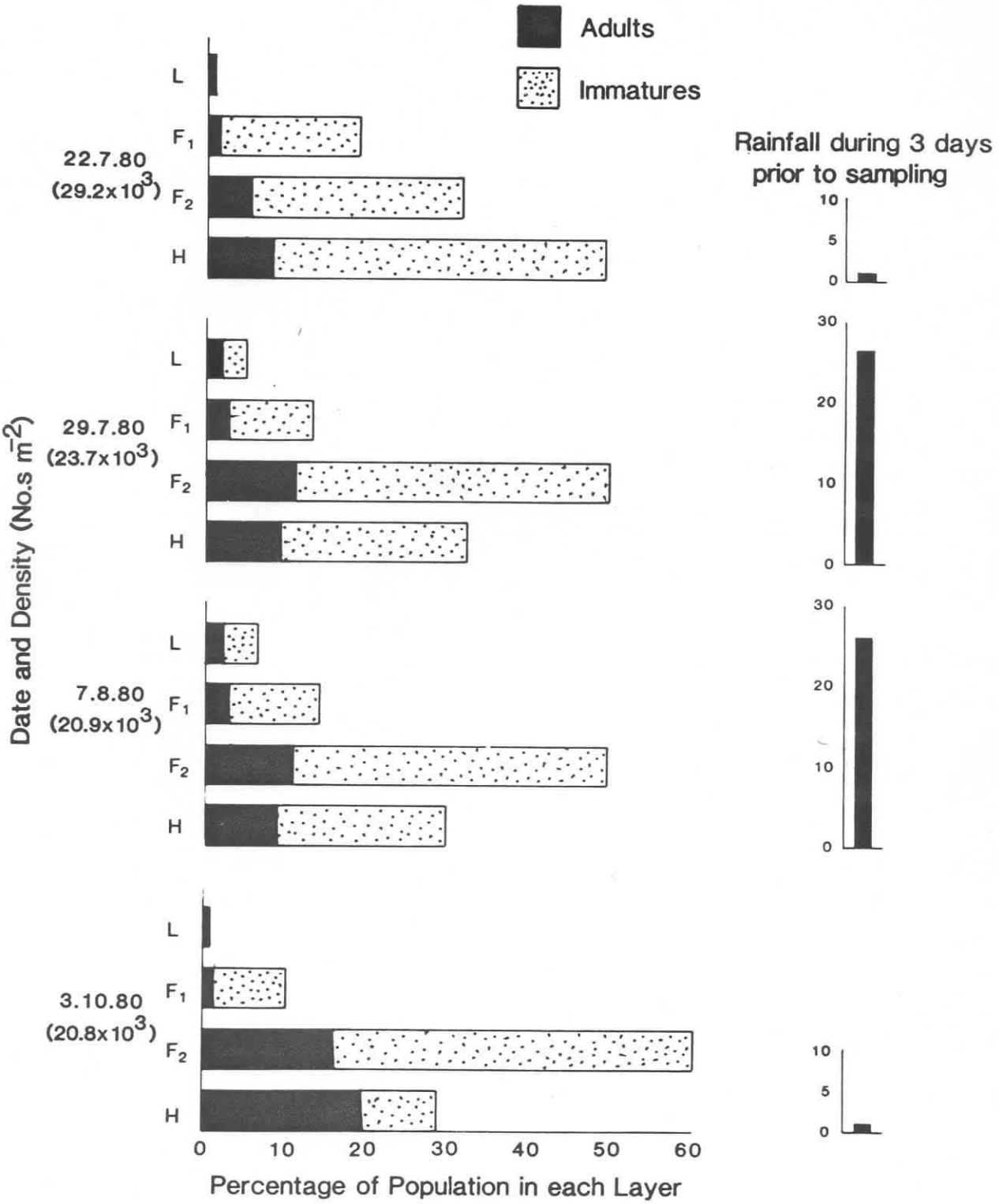


Fig. 1. Vertical distribution of *Onychiurus subtenuis* in the litter profile of a *Populus tremuloides* woodland.

than into four of the five inoculated treatments (where on average 86.2 had migrated into the litter) and again most were on the lowest surface of the autoclaved litter adjacent to the humus. This experiment clearly shows how rapidly these migrations occur as animals had reached the very top surface in the profile within 13 h in 3 of the treatments. There were differences between the different groups, as nearly twice as many animals migrated into the yeast inoculated litter as into the bacteria ($t = 2.43$, $P < 0.05$) or *Mortierella* ($t = 2.92$, $P < 0.02$) inoculated leaves. *Cladosporium*, shown by VISSER & WHITTAKER (1977) to be a preferred food species, attracted the next highest number of Collembola which climbed

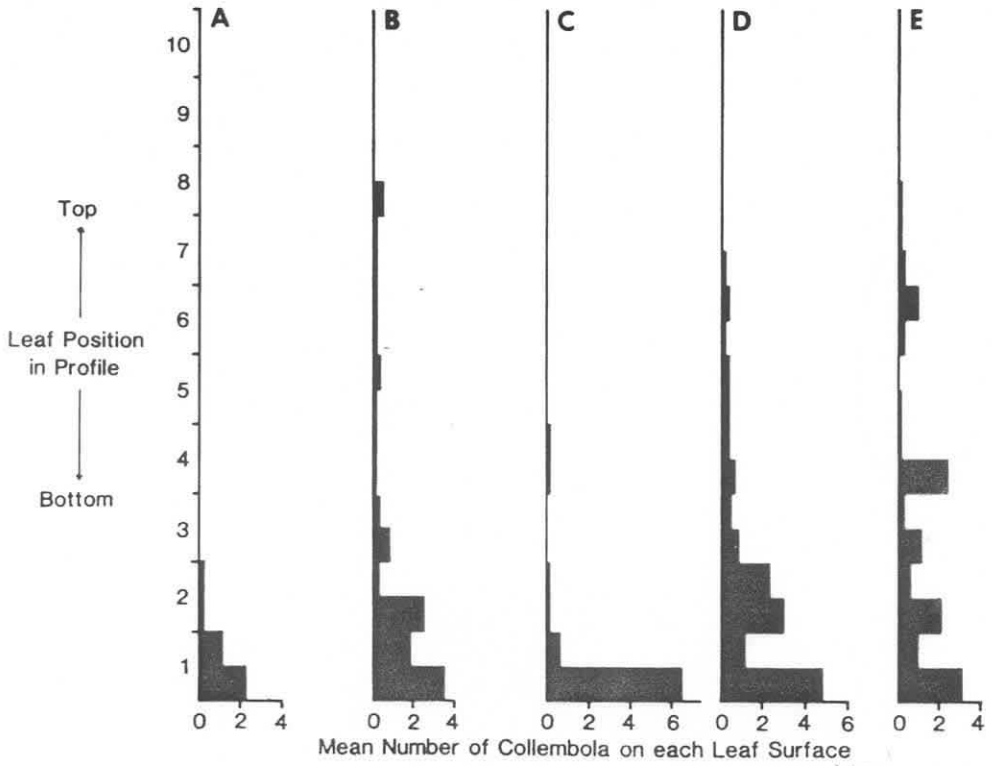


Fig. 2. The distribution of *Onychiurus subtenuis* in microcosm litter profiles 18.5 h after introduction of the leaf laminae. Litter treatments: A, dry; B, moist; C, autoclaved; D, reinoculated with litter microflora; E, reinoculated with humus microflora.

Table 1. Numbers of *O. subtenuis* that had migrated from underlying humus onto leaf laminae 18.5 h after the leaves were placed on top of the humus in laboratory microcosms (n = 6)

Treatment		Dry	Moist	Autoclaved	Litter Microflora	Humus Microflora
Numbers on laminae	$\bar{x}$	3.8	11.7	7.8	14.8	13.3
	S.E.	±1.3	±2.6	±1.0	±2.9	±1.4
Height index	$\bar{x}$	1.89	3.99	1.47	3.56	4.74
	S.E.	±0.31	±0.84	±0.24	±0.56	±0.59

Table 2. Numbers of *O. subtenuis* that had migrated from underlying humus onto leaf laminae inoculated with various micro-organisms 13 h after the leaves had been placed on top of the humus in laboratory microcosms (n = 5)

Treatment		Control	Basidiomycete 290	Bacteria	*Mortierella*	*Cladosporium*	Yeast
Numbers on laminae	$\bar{x}$	31.6	9.6	68.0	63.2	90.6	123.0
	S.E.	±4.5	±1.5	±15.2	±12.0	±7.1	±15.7
Height index	$\bar{x}$	2.57	1.57	4.30	3.45	5.00	3.40
	S.E.	0.16	0.25	0.37	0.51	±0.23	±0.24

higher up this profile than any of the others. (Comparing the height index with that for yeast, $t = 4.14$, $P < 0.01$, and with that for *Mortierella*, $t = 2.47$, $P < 0.05$). However the most conspicuous result was with leaves inoculated with Basidiomycete 290 into which even fewer animals migrated than they did into the control litter ($t = 4.57$, $P < 0.002$) and all were on the bottom leaves of the profile resulting in a height index significantly lower than that for the control ($t = 2.99$, $P < 0.02$).

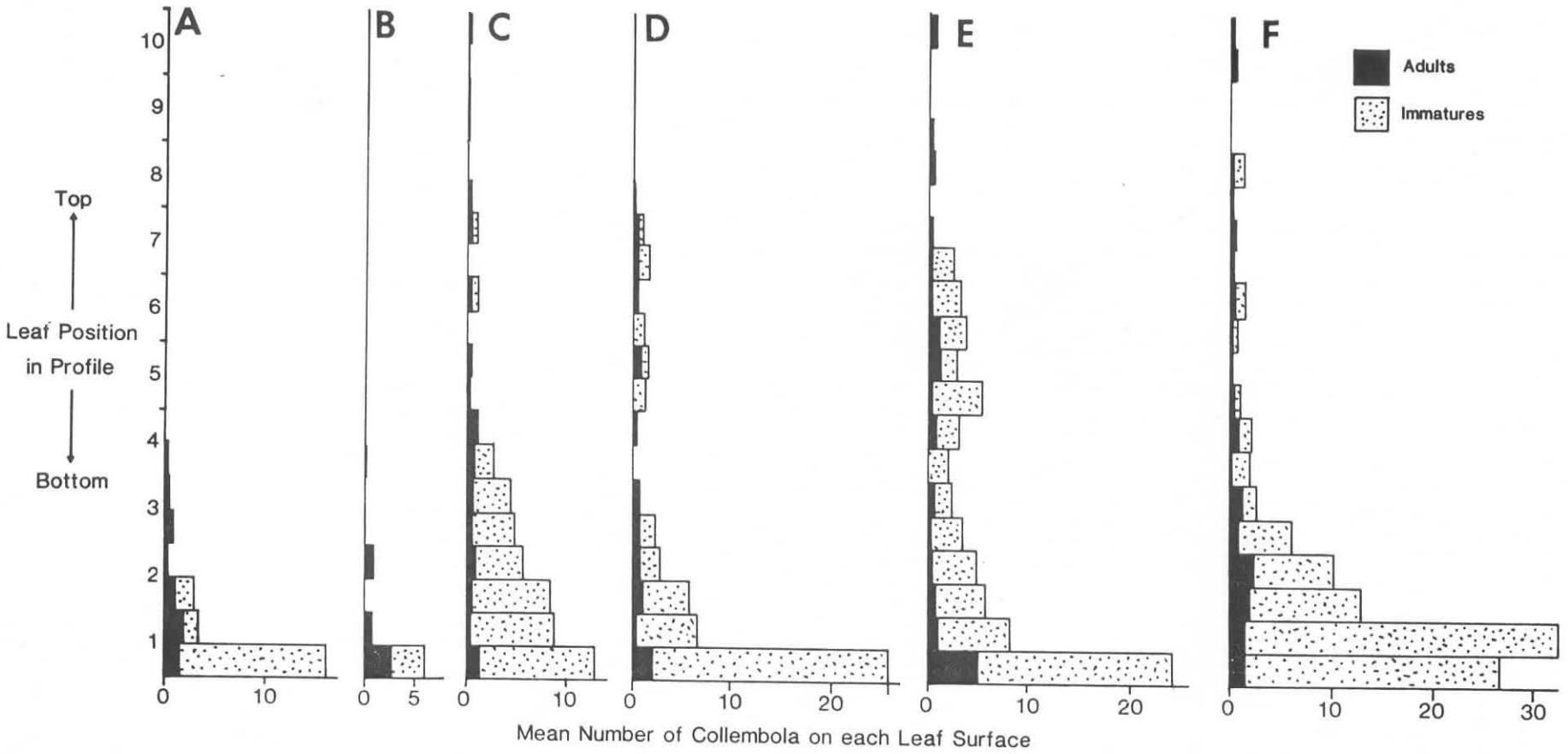


Fig. 3. The distribution of *Onychiurus subtenuis* in microcosm litter profiles 13 h after introduction of leaf laminae that had been autoclaved and reinoculated with various micro-organisms. Leaf tretaments: A, control; B, Basidiomycete 290; C, Bacteria; D, *Mortierella*; E, *Cladosporium*; F, Yeast.

4. Discussion

Results of the field studies show that *Onychiurus subtenuis*, like other species of Collembola, moves into the lower layers of the litter profile during the summer to avoid desiccation (Marshall 1974; Takeda 1978). However, as in the desert ecosystem studied by Whitford *et al.* (1981), these Collembola can return very rapidly to the litter layer following summer rainstorms, over 1,000 m^{-2} moved into the litter until it dried out again 1—2 days later. Field studies cannot however show whether such movements are simply an extension of their foraging activities when the physical limits set by their physiological constraints are relaxed, or whether they are positively attracted into the litter by the burst of microbial activity that occurs when it is remoistened (Whitkamp 1966).

The laboratory studies indicate that the micro-organisms are important in influencing this movement because significantly more animals moved into reinoculated litter than into uninoculated substrates in both experiments. However it is still not clear why they should migrate from a microbially rich humus, several centimetres into the litter only to descend again a few days later when it dries out. Results of the second experiment suggest a possible reason: the Collembola responded more to some species of micro-organism than to others. It is likely that the litter microflora, with a predominance of rapidly sporulating species, is more palatable than are the fungi characteristic of the humus layer. McMillan (1976) has shown that *Onychiurus armata* (Tullb.) Gisin prefers feeding on fungal spores rather than on hyphae, and Visser & Whittaker (1977) have clearly shown that *O. subtenuis* prefers grazing on pigmented fungi such as *Cladosporium* and sterile dark forms to hyaline basidiomycetes. As natural selection favours individuals which can choose a diet that results in increased fitness, and Booth & Anderson (1977) have shown that food quality does markedly affect reproductive output in Collembola, it is probable that the benefits to growth and fecundity derived from migrating up to feed in the litter layer outweigh the metabolic costs of the movement and the added risk of being stranded there when the leaves dry out again.

The conspicuous lack of migration into the litter inoculated with Basidiomycete 290, a species known to be both very unpalatable and potentially lethal to *O. subtenuis* (Visser & Whittaker 1977), supports these conclusions but raises the question of how Collembola in the humus layer detect the presence and activity of micro-organisms higher up the profile. Parkinson, Visser & Whittaker (1979) concluded that Basidiomycete 290 emitted a toxic volatile substance when they observed very high mortalities in experimental treatments in which *O. subtenuis* was enclosed with this species. If this is so it would explain why so few animals migrated into the litter inoculated with Basidiomycete 290. Similarly the strong positive responses to the other micro-organisms could have been due to release of volatile but attractive chemicals.

That such a high proportion (up to 30%) of the population moved so rapidly (within 13 to 18 h) out of the humus confirmed that they were not simply responding to the increased availability of physically suitable habitat but were actively and positively responding to the presence of the microflora in remoistened litter.

Visser, Hassall & Parkinson (unpublished) have shown that *O. subtenuis* from this study site carry spores from 120 different fungal taxa, so by moving vertically through the litter profile in response to microbial activity they may also be dispersing microbial spores to new substrate surfaces.

5. Acknowledgements

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Changes in the vertical distribution of the Collembolan *Onychiurus subtenuis* were observed in the litter layers of a *Populus tremuloides* woodland in Alberta, Canada during summer and autumn. Field studies showed that the Collembola moved down into the deeper horizons of the litter profile during the dry summer months but that a significant proportion of the population returned to the surface litter layers within a few hours after summer rain storms and remained to feed there until the litter dried out again.

Laboratory experiments with artificial litter profiles showed that this vertical migration occurred in response to the presence of micro-organisms growing on the surfaces of leaves in the litter layer and that it was not simply a response to an increase in availability of suitably moist habitat. The laboratory experiments also revealed that *O. subtenuis* responds differently to different groups of micro-organisms. Significantly more Collembola moved into leaves inoculated with yeasts, and significantly higher up into leaves inoculated with *Cladosporium*, than into leaves inoculated with *Mortierella* or bacteria. Leaves inoculated with Basidiomycete 290 were repellent to the Collembola.

The laboratory experiments suggest that the reasons for the vertical migrations observed after summer rainstorms are related to the presence in the litter layer of micro-organisms which have a higher nutritional quality than those growing in the humus layer.

Key words: faunal-microbe interactions, vertical migration, optimal feeding strategy, fungi, spore dispersal, *Onychiurus subtenuis*.